ON THE HISTOLOGICAL STRUCTURE OF SOME AUSTRALIAN GALLS.

By E. Küster, Hon. F.R.M.S. (London), Professor of Botany, Giessen (Germany).

(Fourteen Text-figures.)

[Read 28th April, 1937.]

The galls of the Australian flora have been often subjected to detailed investigations—from Schrader (1863) and Rübsaamen (1894) to numerous studies of Froggatt.

The interest taken in the Australian galls is founded not only on the novelty of the objects, which promise a great many details yet undiscovered, compared with the relatively well investigated European and North American galls. In addition to the descriptive studies and catalogues there are important points of view of general biology: the botanist is interested in the Australian galls because they are associated with host-plants different from those in the European and North American floras; the zoologist confirms that Coccidae are responsible for a great part of the Australian galls, but these play an unimportant part in the northern hemisphere.

The general cecidology has developed through the study of the galls of the European flora. The Cynipid galls of *Quercus* have made known a great many highly complicated morphological and histological differentiations which cannot be attained by the productions of other gall-making insects in Europe or in North America, and they overshadow the productions of other host-plants of the Hymenoptera through their variety of structure. Therefore we have long been accustomed to consider the Cynipid gall of *Quercus* as the chief object of the general cecidology.

The questions which concern the botanist have hardly been considered in connection with the Australian Eucalyptus galls. The botanical communications are hardly more than descriptions of the exterior form of the galls. Consideration of the cytological and histological structure of the galls is completely wanting, although most important results can be expected from their investigation.

Some results which concern the anatomy of the Australian galls are described herewith, although I know very well that distance hinders me from detailed investigation of living and ontogenetic material, and so I can only touch on many important questions.

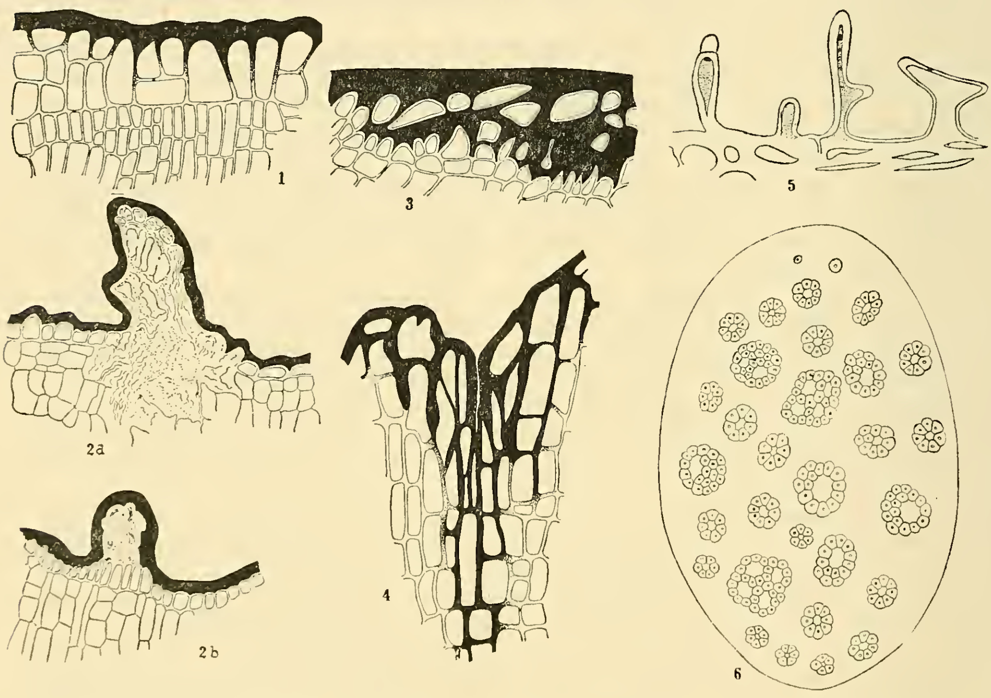
A great many of the galls which I have studied belong to Coccidae. These productions are not inferior to the highly organized productions of Cynipidae, either in exterior form or in histological structure. The histological structure of the galls of Coccidae promises important and surprising results, and so I should like to recommend its study very strongly to Australian cecidologists and phytopathologists.

The following pages perhaps give a few suggestions for future detailed investigations.

Epidermis.

In the "inclosed" galls, i.e., in those whose epidermis develops ontogenetically directly from the epidermis of the mother organ, the epidermis is usually equal or very similar to the normal tissue. Noteworthy is often the strong upward growth of the cells, so that they take the form of narrow palisades; it sometimes happens that palisades divide themselves by pericline walls and the epidermis becomes locally a double or multiple layer; figure 1 shows part of a gall, in which the cells of the epidermis are highly developed and grow as a cushion in the fundamental tissue. Such features are not common in galls.

The cuticle of many foliar galls is much thicker than the normal one. On concavely curved divisions of a coccid gall I noticed the formation of folds of the surface: there are narrow ridges consisting either of folded epidermis matter rising from the fundamental tissue (Fig. 2*a*) or simply of cuticle which here and there frees itself from the epidermis cells and rises in folds; under the cuticle one sees small remains of membrane, lower still the epidermis (Fig. 2*b*).



"Cuticularepithel" (Damm) has been observed sometimes in the galls (Küster). Especially strong, many-layered and varying, I have found it in many Coccid galls of the eucalypts; particularly near small wounds, but apparently also independent of such, the upper layer of fundamental tissue is cutinized; the cells become similar to the epidermis so that one seems to see two typical and strongly cutinized epidermis layers; also the third and fourth tissue layer may be cutinized (Fig. 3).

An unusual form of "cuticularepithel" I have found in those leaf galls in which the growth of the fundamental tissue is impeded here and there—perhaps through a small trauma—and a deep notch in the cushion of the gall tissue. In the surface of the gall tissue brought together one finds a cuticularepithel in further development (Fig. 4).

Free galls, i.e., such as develop from the interior of the mother and whose epidermis may be considered as a new formation, do not seem to be lacking in the Coccid galls of eucalypts. It seems impossible to work on this important question without ontogenetic material. I recommend this problem for detailed studies.

In galls which I supposed to be free, I have repeatedly noticed luxurious cork formation in the physiological trauma of the point of rupture.

In comparison with the *Quercus* galls and many other features of the European gall flora, I mention that the Eucalypt galls are smooth; only in one gall have I observed uni- or pluricellular, simple or rarely T-shaped, branched albuminous hairs, developed on the interior surface. I am unable to say whether they arise from a typical epidermis or from a fundamental tissue-like matter whose surface cells sometimes stretch themselves tube-like (Fig. 5).

Bundles.

In many Eucalyptus galls the bundles have the same loose net-like distribution which is well known from the Pontania galls and many Cynipidae productions of the European flora. I have nothing remarkable to report on the structure of the delicate bundles as I have found them in many Australian galls.

In several Coccid galls the development of highly differentiated and characteristically distributed bundles is surprising.

As first example, I mention the bundles of the long processes of the well-known gall of *Brachyscelis munita*. In the cross section (Fig. 6) there are about 40 bundles regularly distributed and parallel to one another; one finds large bundles next to small ones, single ones next to small groups composed of 2–4 bundles. The distribution is somewhat similar to the structure of monocotyledonous stems; however, the frequent very striking accumulation of the bundles in the periphery is lacking.

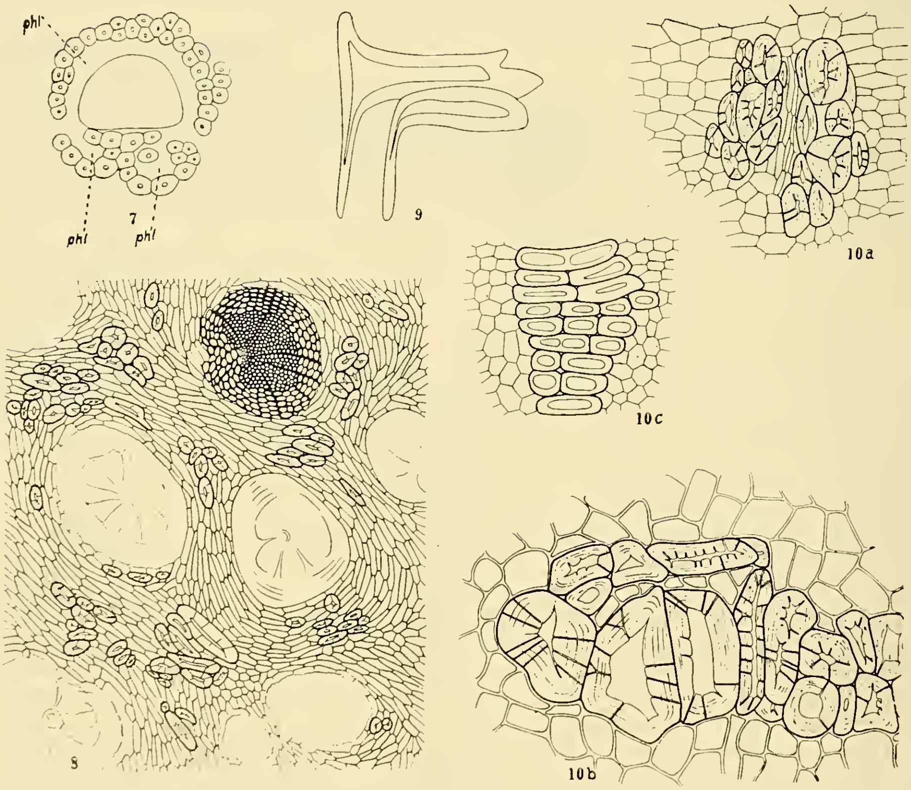
The structure of the single bundles is characterized by the collateral distribution of xylem and phloem; it is difficult to determine whether small phloem divisions exist, corresponding to the intra-xylary phloem of the Myrtaceae and to the structure of the bicollateral bundles; the bundles are too small; one can, however, definitely say that sometimes isolated groups of phloem-like cells are to be found (Fig. 7) between the sclerenchyma.

The orientation of the phloem is not determined by that of the bundles in the cross-section of the gall-organs; the phloem is not always orientated outwards. But when several bundles unite in a small group, the phloem of the single bundle is always orientated toward the periphery of the small group.

All bundles are enveloped by bast fibres (Fig. 6). These form a ring, mostly uninterrupted round the bundles, and sometimes enclose also the above-mentioned isolated phloem-like groups (Fig. 7). The bast-fibre shoot is generally one cell-layer thick; more rarely one finds two or three layers.

When the bundles unite in groups in this way, so that they touch one another, and when no fundamental tissue layers remain between them, the bundle tissues are divided from the bast-fibre layers in 2, 3 or 4 compartments; sometimes the division remains incomplete, in which case one sees a bast-fibre septum push itself only as far as the centre of the bundle tissue.

As second example, I take the bundles of a gall which is similar to (or identical with) the gall of *Brachyscelis conica.* In the urn-shaped body of the galls, several centimetres long, numerous bundles are to be seen. These are remarkable because of their richness in secondary tissues; they form radially-structured concentric or excentric masses, which enclose in the centre of growth a very small, perhaps phloem-like, cell-group. The wood-cylinder consists especially of cells arranged in regular radial rows, and is streaked by pith rays (Fig. 8). In the largest bundles the longest radii are about 20 cells long; it is difficult to demonstrate phloem beyond the xylem cylinder; in many cases the outside xylem cells touch directly fundamental tissue cells, in others a thin layer of a phloem-like tissue is to be seen. To describe the ontogeny of the bundles was impossible with my material; especially I was not able to decide whether, in the phase before me, the bundles had everywhere finished the production of secondary tissue or not.



The histological structure of these bundles is characterized in the first place by the regular radial distribution of the elements. There are found the characteristics well known in many other wound-wood and gall-wood features (in wood = knots and "Kugeltrieben"; Küster, 1925). Sometimes a difference is seen between thin-walled exterior and thick-walled interior cells between which an annular ring-like boundary line is noticed. In many other cases, single broad or narrow sectors are differentiated from the greater part of the bundles by their structure orientating their elements, not in the longitudinal axes of the bundles, but perpendicular to them.

If the thickening of the bundles is anywhere impeded, contours of the woodbody arise as they are known from the carcinoma features of the trees.

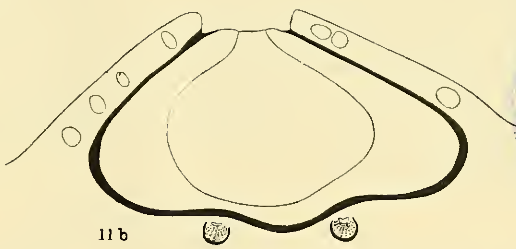
Every bundle which is capable of such strong growth may be considered a small stele. This form of anomalous thickening is unknown to me in other galls.

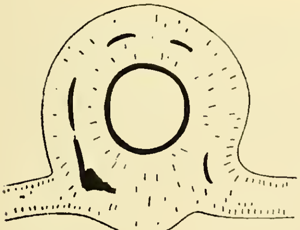
Stone cells.

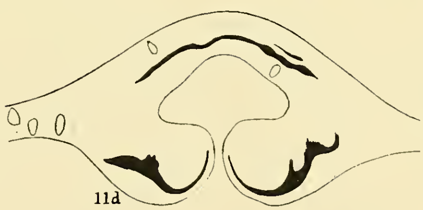
As with the galls of many Diptera and Hymenoptera, also many of the Coccid galls are very rich in stone cells.

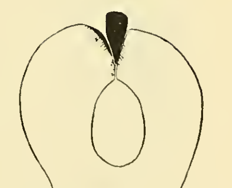
As in those, we find also in Coccid galls stone cells of various forms and wall qualities—relatively thin and thick-walled, thickened on all or one side. Stone cells of the second species are known to the European and American cecidologists, particularly from very numerous oak galls (Weidel), also from *Salix* and other galls (Küster). An ontogenetic examination of the stone cells of the Eucalypt galls from Weidel's point of view is greatly to be desired. I was not able to determine from the material before me whether all galls provided with stone cells thickened on one side are produced by Coccids; perhaps some of them were produced by Cynipids; in any case, it is certain that stone cells thickened on one side occur also in Coccid galls.

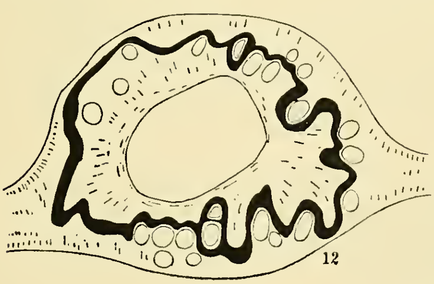

11a

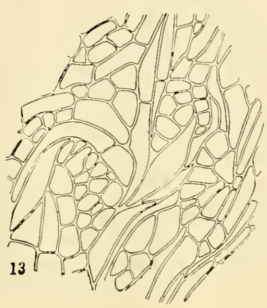

11b

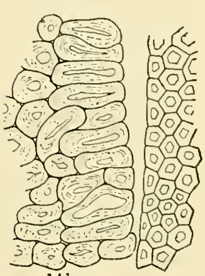

11c


11d


14a


12


13


14b

I repeatedly noticed in Eucalypt galls stone cells, which were spherical or palisade-like, formed and at some points were provided with long thread-like processes (Fig. 9). It has been long known from normal and pathological anatomy that stone cells push between neighbouring cells with pointed thorn-like forms; the Australian specimens here in question were noticeable to me as the processes developed in the direction perpendicular to the surface of the gall-bearing organ and towards the strongest normal tissue growth.

Very striking is the circumstance in many Eucalypt galls, that in transverse and longitudinal section the stone cells form round-contoured or spindle-like groups (Fig. 10); there is no doubt that the cells united in a group are descendants of one mother-cell.

The distribution of the stone cells in the tissues of the Coccid galls follows the principle well known from many other anatomically carefully investigated galls: either the stone cells are singly placed or united in small groups in the thin-walled fundamental tissue or they form continuous zones ("mechanische Mäntel") in the later phases of the cecidogenesis. One often sees thin-walled fundamental tissue become somewhat thick walled and equally lignified.

Figure 11 shows some Coccid galls and their mechanical zones. From the ontogenetic point of view, especially interesting are the galls in which the larva-cavities are surrounded by abundant thin-walled tissue and the exterior layers are formed of parenchyma filled with oil receptacles. The stone-cell zones develop at the junction between the exterior and interior parenchyma; noteworthy features result, if an exaggerated growth of the exterior parenchyma compels the contour of the mechanical zone to rupture or "Verwerfung" (Fig. 11*a*).

In some galls oil receptacles are found only beyond the thick-walled zones and are very closely accumulated; the mechanical tissue layers push themselves here and there between neighbouring oil receptacles and can enclose these imperfectly (Fig. 12).

Oil Receptacles.

To the most important anatomical characters of *Eucalyptus* belong the oil receptacles. They play a large part in the galls of *Eucalyptus.* I have earlier (Küster, 1900) demonstrated that the Eucalypt galls are differentiated greatly through the richness of their oil receptacles: I found galls containing only a few receptacles or completely lacking in them—to the latter belong several foliar galls of Eucalyptus which remind one, through the production of "emergences", of the "Erineum populinum" among others, and which may be considered through their morphological characters—merely as conjecture—as mite galls.

The size of the oil receptacles in galls often exceeds the normal. I saw, in some Coccid galls, receptacles of which the diameter was 380μ; in oval receptacles the longest diameter was even 540μ. On the other hand, one also meets extraordinary small receptacles in Eucalypt galls, and in some others large and small ones irregularly mixed. An ontogenetic examination, particularly of the small receptacles, would certainly be of great interest and promises various noteworthy additions to Fohn's results.

The position of the oil receptacles varies. I have found galls in which all layers show receptacles, so that they lay, in some parts, in 6–8 layers. I found others in which the receptacles are to be seen directly beneath the epidermis and sometimes push it out hemispherically. Sometimes the receptacles lay so compactly that only narrow tissue remains lay between them.

The histology of the oil receptacles of *Eucalyptus* galls shows various notable features. Their form is sometimes determined by the growth in the neighbourhood; between exceptionally elongated cells the receptacles assume a form in the same direction extended, sometimes like a bottle-neck. The cells of the epithelium are often very large and arched; they fill the lumina of the receptacles with ball- or tube-like forms. It would be very important to examine the physiology of those receptacles whose epithelium has become thick walled. I have never noticed sclerosis, pits, lignification in the cells of the epithelium; in one of the galls which I examined, the tissue surrounding the receptacles so perfectly devolved on sclerosis that the receptacles were almost completely enclosed by thick-walled lignified tissue (Fig. 12); however, the cells directly enveloping the lumina of the receptacles (epithelium) take no part in the sclerosis.

The great abundance of receptacles in many galls suggests the importance of a comparative chemical examination of the oil which is produced in the galls and in the normal leaves of *Eucalyptus* (cf. Salgues, 1936).

Secondary tissues.

Voluminous masses of secondary tissues develop through the gall infection out of the normal cambium ring of the stems. The abnormal wood forms thick layers, the structure of which equals that of other gall-wood features and is characterized especially by the shortness of its elements. Figure 13 shows a longitudinal section of the secondary gall wood. A great part of the wood consists of thick-walled parenchyma, between which run short fibre-like elements—sometimes straight, sometimes curved, rarely fork-like branched.

Also secondary phloem is formed abundantly through some gall infections; sometimes I was struck by the very clear stratification; I counted 14 layers of stone cells which alternated with thin-walled phloem.

Cork patches and spherical cork nests occur in the galls, as in the normal *Eucalyptus* organs, after local necrosis and local trauma.

Necrosis; cytolysis.

Dry necrosis is in some galls the result of interior suberization, through which the outward layers of gall tissues die off. Occasionally the symptoms of the dry necrosis become especially interesting through position and form and through the histological metamorphosis of the dying tissue divisions and the neighbouring layers. Figure 14 shows in the vertex of the gall a stopper-like necrotic part whose cells are very thick walled; the directly adjacent layer consists of long palisade-like cells.

Lignification of tissues is by no means rare in galls (Lysenchyma—Weidel, Küster). In the galls of *Eucalyptus* one meets symptoms of lignification or cytolysis very often. The cytolysis does not characterize fixed phases of the gall evolution or fixed tissues; rather, one often sees small groups of primary and of secondary gall tissues dead and lignified—similar to the case of the gummosis. Detailed examination of the phenomena seems very desirable.

I am indebted to Miss Fawcett, of Melbourne, for the opportunity to examine a great number of Australian Eucalyptus galls. I offer her my best thanks for her kind assistance; she has sent me countless well preserved samples.

The above comments give a report on my investigation of the material provided by Miss Fawcett. I publish them in the hope of giving my Australian colleagues suggestions for more careful investigation of the galls of Australia which have hardly been considered botanically.

Literature.

FOHN, N., 1935.—Zur Entstehung und Weiterbildung der Exkreträume von *Citrus medica* L. und *Eucalyptus globulus* Kab. *Österr. Botan. Zeits.*, Bd. 84, p. 198.

FROGGATT, W. W., 1916.—A descriptive catalogue of the scale insects ("Coccidae") of Australia. *Agric. Gaz. N. S. Wales*, vol. 27, p. 425.

HOUARD, C., 1922.—Les Zoocécidies des plantes d'Afrique, d'Asie et d'Océanie. Vol. 2. Paris.

KÜSTER, E., 1900.—Beiträge zur Anatomie der Gallen. *Flora*, Bd. 87, p. 118.

————, 1911.—Die Gallen der Pflanzen. Leipzig.

————, 1925.—Pathologische Pflanzenanatomie. 3rd edit. Jena.

————, 1930.—Anatomie der Gallen. Linsbauer's Handbuch der Pflanzenanatomie. Lief. 26, Berlin.

————, 1935.—Die Pflanzenzelle. Jena.

RÜBSAAMEN, EW. H., 1894.—Über Australische Zoocecidien und deren Erzeuger. *Berl. Entom. Zeits.*, Bd. 39, p. 199.

SALGUES, R., 1936.—Sur l'huile essentielle des hampes florales d'origine parasitaire. *C.R. Soc. Biol. Paris*, vol. 121, p. 1074.

SCHRADER, H. L., 1863.—Über gallenbildenden Insekten in Australien. *Verh. Zool.-Bot. Gesellsch. Wien*, Bd. 13, p. 189.

WEIDEL, F., 1911.—Beiträge zur entwicklungsgeschichtlichen und vergleichenden Anatomie der Zynipidengallen der Eiche. *Flora*, Bd. 102, p. 279.